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Food and energy processing by Oribatid Mites

BY

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INTRODUCTION

Information on the nutritional biology of oribatids has been reviewed by LUXTON (1972), who classified their feeding according to food selectivity. Thus, some oribatids are macrophytophages (consuming the remains of higher plant material), others are microphytophages (preferring to eat microbial material), and yet others panphytophages (having attributes of each of the first two). Their functional ecology is conveniently discussed in terms of these broad groupings, since their ecological role (LUXTON, 1972), the duration of their life-cycle and their fecundity (SAICHUAE *et al.*, 1972), and their distribution patterns (PANDE and BERTHET, 1975) are determined by their feeding preferences.

Subsequent work on oribatid nutrition has included that of WEBB and ELMES (1972), DINSDALE (1974 a, 1974 b), NANNELLI (1974), STEIGEN *et al.* (1975), STEFANIAK and SENICZAK (1976) and SCHULTE (1976), but little of this work has dealt in detail with quantitative aspects.

DIGESTION

ZINKLER (1971, 1972) and LUXTON (1972) have shown the presence of a wide range of carbohydrase enzymes in oribatids, distributed among the species according to their feeding habit (Tab. I). Macrophytophages in general possess cellulase but not trehalase (trehalose is a common storage carbohydrate of fungi), whereas the microphytophages possess trehalase but not cellulase. DINSDALE (1974 a) has further noted high carbohydrase activity and the pre-

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sence of proteases (detectable only with the most sensitive of tests) and lipases in the gut of a species of *Phthiracarus*. DINSDALE found that α and β glucosidase activity was restricted to the ventriculus and its associated caecae, and that the enzymes of the gut lumen were of secondary importance to the surface activity of the gut mucosa. Furthermore, specialised secretory glands in the gut wall were absent, and there appeared to be an intracellular mecha-

TAB. I

Carbohydrases in oribatid mites

	MACROPHYTOPHAGES					PANPHYTOPHAGES										MICROPHYTOPHAGES						
	S. magnus (1)	*S. magnus* (2)	*S. spinosus* (1)	*P. piger* (2)	*Phthiracarus sp.* (3)	*A. coleoptrata* (1)	*H. initialis* (1)	*A. ovalus* (1)	*L. subterraneus* (2)	*X. tegeocranus* (1)	*C. gracilis* (1)	*E. seminulum* (2)	*N. palustris* (1)	*N. silvestris* (2)	*N. silvestris* (1)	Nothridae juvs. (1)	*B. corynopus* (1)	*D. clavipes* (1)	*Damaeus* juvs. (1)	*D. auritus* (2)	*A. troisii* (2)	*E. plicatus* (2)	*H. rufulus* (1)
α glucosides																							
maltose	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
sucrose	+	0	—	0	+	+	+	+	0	+	+	0	+	0	+	+	+	+	+	0	0	0	+
melezitose	—	0	?	0	+	—	—	?	0	+	+	0	+	0	+	+	+	+	+	0	0	0	—
trehalose	—	+	—	+	—	—	+	?	+	+	+	—	+	+	+	+	+	+	+	+	+	+	+
β glucosides																							
cellobiose	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
salicin	+	0	+	0	0	+	+	+	0	+	+	0	+	0	+	+	+	—	+	0	0	0	+
α galactosides																							
raffinose	?	0	?	0	+	+	+	+	0	+	+	0	+	0	+	+	+	+	+	0	0	0	+
melibiose	+	+	+	—	+	+	+	+	+	+	+	+	+	+	+	+	—	—	—	+	+	+	—
β galactosides																							
lactose	—	+	—	+	—	—	—	—	+	—	—	+	—	+	—	—	—	—	—	+	—	?	—
polysaccharides																							
amylose	?	+	+	+	+	?	—	?	+	+	+	+	+	+	+	+	+	?	+	+	+	+	+
cellulose	+	—	+	—	—	+	+	+	?	+	+	+	+	—	+	+	—	—	—	—	—	—	—
pectin	+	+	+	+	0	+	?	?	+	+	+	+	+	+	+	+	—	—	—	—	—	—	—
xylan	+	+	+	+	0	+	+	+	+	+	+	+	+	+	+	+	—	—	—	—	—	—	—
chitin	?	0	—	0	—	—	+	—	0	—	?	0	?	0	?	—	?	?	?	0	0	0	?
galactan	—	0	—	0	0	—	—	—	0	—	—	0	—	0	—	—	—	—	—	0	0	0	—

+ = present
— = absent
? = not certain
O = not measured
(1) Luxton, 1972 ; (2) Zinkler, 1972 ; (3) Dinsdale, 1974.

nism for the digestion of proteins at least. DINSDALE suggests that most polysaccharides are hydrolysed at the brushborder of the gut epithelium or in the gut lumen itself. According to DINSDALE food particles are rarely found in the caecae although their walls are invaginated and they may have a role to play in the removal of catabolites from the haemolymph. However, SCHULTE (1976), working with the microphytophage *Ameronothrus*, states that finer particles are sorted from the gut content and are passed to these caecae.

Several authors (e.g. WOODRING, 1963; ENGELMANN, 1961) have noted the presence of possible microbial symbionts in the guts of oribatid mites, a presence which might account for the measured cellulolytic activity in the guts of some species. *Phthiracarus* appears to be unable to digest cellulose, and DINSDALE (1974 a) noted possible bacterial symbionts in the caecae of very few (about 8 %) of his sectioned specimens. On the other hand, STEFANIAK and SENICZAK (1976) noted that the alimentary canals of *Achipteria coleoptrata* (especially those of juveniles) contained a fairly rich bacterial flora with a high proteolytic and cellulolytic activity.

FOOD ENERGY PROCESSING

The view has been stated many times in the literature that the 'poor quality' of food available to macrophytophagous animals will give rise to low efficiencies of digestion. The oribatids of this group tend to attack only partially decayed material (HARTENSTEIN, 1962; HAYES, 1963; NANNELLI, 1974) presumably because the microbes condition it in some way for them. In the absence of a trehalase it seems unlikly that the animals digest much of the microbial material contained in the food and, in any case, since fungal material is readily available as food without the energy-consuming task of excavating leaves or wood, it seems unlikely that the macrophytophagous habit would have evolved among the soil oribatids merely as a means of exploiting only microbial energy reserves. Although there appear to be few readily digestible substances remaining in decayed litter, except for cell wall material, the macrophytophagous oribatids are well-adapted to exploit simpler carbohydrates released by microbial activity and also to digest part of the higher plant material itself. The microphytophages exploit a more readily available food resource and the panphytophages (to which the majority of oribatids belong) are adapted to utilise a wide range of substrates.

a) **Consumption.**

Figures for oribatid consumption rates are given in Table II. They vary between 1 and 13 % of dry body weight ingested per day, with a single high figure of 25 %. The only comparative data for adults and juveniles of the same species *(Damaeus clavipes)* are given by LUXTON (1972). He indicates that, per individual, adults are able to process by far the most material, although amounts consumed per unit body weight remain quite similar throughout the developmental stages. The amount ingested seems to decrease with the age of the adult (WOODRING, 1963; WEBB and ELMES, 1972).

TAB. II

Consumption rates among oribatids

Species	% dry body wt. ingested day^{-1}	Food	T° C	Authority
Cultroribula juncta	25	*Pinus* litter	20	Kowal 1969
Camisiidae	2.3	*Liriodendron* litter fungi	Field	McBrayer and Reichle 1971
Carabodidae	2.5	*Liriodendron* litter fungi	Field	McBrayer and Reichle 1971
Cymbaeremaeidae	9	*Liriodendron* litter fungi	Field	McBrayer and Reichle 1971
Damaeus clavipes				
adults	9	Fungal mycelium	15	Luxton 1972
tritonymphs	5.5	Fungal mycelium	15	Luxton 1972
deutonymphs	7	Fungal mycelium	15	Luxton 1972
protonymphs	9	Fungal mycelium	15	Luxton 1972
Epilohmanniidae	1	*Liriodendron* litter fungi	Field	McBrayer and Reichle 1971
Palaeacaridae	1	*Liriodendron* litter fungi	Field	McBrayer and Reichle 1971
Oribatulidae	1.7	*Liriodendron* litter fungi	Field	McBrayer and Reichle 1971
Phthiracaridae	1	*Liriodendron* litter	Field	McBrayer and Reichle 1971
Steganacarus magnus	2-4	*Fagus* litter *Corylus* litter	18	Berthet 1964
Steganacarus magnus	3-8	*Calluna* litter	18	Webb and Elmes 1972
Steganacarus magnus	5	*Fraxinus* litter	15	Luxton
Cryptostigmata adults	12.5	*Pinus* litter	Field	Kowal and Crossley 1971
Cryptostigmata immatures	5.9	*Pinus* litter	Field	Kowal and Crossley 1971
Cryptostigmata adults	1.4	*Pinus* litter	6	Kowal and Crossley 1971
Cryptostigmata immatures	2.6	*Pinus* litter	6	Kowal and Crossley 1971
Cryptostigmata adults	4.6	*Pinus* litter	15	Kowal and Crossley 1971
Cryptostigmata immatures	2	*Pinus* litter	15	Kowal and Crossley 1971
Cryptostigmata adults	13.3	*Pinus* litter	25	Kowal and Crossley 1971
Cryptostigmata immatures	7.6	*Pinus* litter	25	Kowal and Crossley 1971

Although it still remains true that the feeding habits of juveniles make a significant contribution to total oribatid ingestion, it must also be remembered that a rather large amount of time (35-86 %) is spent in ecdysis or moulting preparation by juveniles when they will not be feeding (HARDING and STUTTARD, 1974). Furthermore, ingestion rate may vary seasonally and WITKAMP (1960) has stated that in winter this rate may be one-quarter to one-third of that in summer.

b) **Assimilation.**

A list of assimilation efficiencies among oribatid mites is given in Table III. The range extends from 10 to 66 % with most of the figures at

TAB. III

Assimilation efficiencies of oribatid mites

Species	Food	T° C	A/C % *cals **weight		Authority
Carabodes labyrinthicus.....	Fungal hyphae	10	40*		Steigen et al 1975
Damaeus clavipes....	Fungal hyphae	15			Luxton 1972
adults.....			62*	62**	
tritonymphs.....			47*	47**	
deutonymphs.....			66*	65**	
protonymphs.....			63*	64**	
Steganacarus magnus	Leaf litter	18	10-15**		Berthet 1964
Steganacarus magnus	Leaf litter	18			Webb and Elmes
mature ♀♀.....			62*	53**	1972
new ♀♀.....			69*	58**	
mature ♂♂.....			41*	19**	
new ♂♂.....			69*	58**	
Steganacarus magnus	Leaf litter	15	49-61**		Luxton

the higher end. It is clear that some macrophytophages may be just as efficient at utilising their preferred food material as are the microphytophages, presumably a function of their wide range of digestive enzymes. There seems to be little variation in assimilation rates and efficiencies between developmental stages of the same species (LUXTON, 1972), although in adults they may diminish with age (WEBB and ELMES, 1972).

c) **Metabolism.**

LUXTON (1975) has summarised the known data on the respiratory metabolism of oribatid mites. Generally speaking the feeding associations appear

to be closely related to the pattern of oxygen uptake, with the macrophytaphages lowest, the panphytophages highest, and the microphytophages at an intermediate level. Q 10 s vary from 2 to 6, with a mean of 3.63, which are rather high for arthropods. Nevertheless, the energy dissipated in metabolism from most woodland and grassland ecosystems by oribatid mites is low at 2-10 kcals $m^{-2}yr^{-1}$ (LUXTON in prep.). Little is known of the relative contribution made by the various developmental stages but WEBB (1969), working with a population of *Nothrus silvestris,* states that the larvae consumed 5 % of the total annual oxygen uptake, protonymphs 7 %, deutonymphs 13 %, tritonymphs 27 %, and adults 48 %.

THEORETICAL ENERGY BUDGETS

Few data have been available in the literature to provide a realistic quantitative balance to the Production Biology Equations:

$$C = A + FU$$
$$A = R + P$$

for any species of oribatid mite. Only the figures of LUXTON (1972, 1975) and WEBB and ELMES (1972) have allowed complete substitution of data for the parameters, and only WEBB and ELMES have provided a complete picture in the literature. Furthermore, the method for obtaining assimilation information in both these instances was based on ^{32}P elimination curves, and hence suspect (HARDING and STUTTARD, 1974). Using ^{32}P simply as a marker, LUXTON (1972) was able to get a remarkably similar comparison with assimilation efficiencies calculated for *Damaeus clavipes* adults by the radioisotope elimination method. Recent work in Liverpool with *Steganacarus magnus* has provided assimilation data using both the ash-ratio method (CONOVER, 1966) and gravimetry, which are extremely close to the figures given by WEBB and ELMES (1972). It is thus with greater confidence that a quantification of energy processing on the part of oribatids can be made (Tab. IV).

In all cases the figures are remarkably similar except that the macrophytophage *(S. magnus)* appears to consume more than the microphytophage *(D. clavipes).* In energetic terms, however, it digests about the same. These two things taken together probably reflect the presence of more recalcitrant material in the macrophytophage diet.

The most interesting figures, however, concern the relative proportions of assimilate contributing to R and P. In all cases the production is distinctly in excess of respiration, even if WIGHTMAN'S (1977) correction factor ($\times$ 2.5) for closed-vessel respirometers is accepted. In general, therefore, oribatids may be assigned to MCNEILL and LAWTON'S (1970) category of 'comparatively short-live poikilotherms showing low respiratory cost stages in which annual population production efficiencies are high'. Possibly oribatids are compelled to store energy in body tissue to see them through adverse or non-feeding periods, and the higher calorific values measured from specimens

TAB. IV

Energy budgets for adult oribatid mites expressed in cals $\times 10^{-3}$ and μg mite^{-1} day^{-1}

Species	Method	T°C	C		A		F		R	P	A/C %	R/A %	P/A %	Authority
			d. wt	cals	d. wt	cals	d. wt	cals	cals	cals				
Steganacarus magnus (combined data)	Radio-isotope	18	9.2	47.1	6.2	29.8	4.6	17.3	2.5	27.3	63	8.4	91.6	Webb and Elmes 1972
Steganacarus magnus	Gravi-metry	15	8.8	39	5.4	23.9	3.4	15.1	4	19.9	61	16.7	83.3	Luxton
Damaeus clavipes	Radio-isotope	15	5.8	26.7	3.6	16.4	2.2	10.3	2.7	14.1	62	16.5	83.5	Luxton 1972

collected in the winter would lend support to this view (WALLWORK, 1971, 1975; LUXTON, 1975). Therefore, although it is conceded that oribatids play an important part in mineralisation processes, their most significant ecological role may well be in their contribution to the regulation of nutrient fluxes within the soil subsystem by virtue of their immobilisation of these nutrients within their tissues for extended periods of time.

SUMMARY

The literature on the nutritional biology of oribatid mites is briefly reviewed, and a Table of carbohydrase enzymes isolated from oribatids is presented. Figures are given for food consumption rates which range between 1 and 13 % of the dry body weight ingested per day. Assimilation efficiencies vary between 10 and 66 % with most at the upper end of the scale. Q 10 s for oribatids vary from 2 to 6 with a mean of 3.63. The energy dissipated in oribatid metabolism from most terrestrial ecosystems is relatively low at 2 - 10 kcals $m^{-2}yr^{-1}$. Full energy budgets are presented for a macrophytophage (*Steganacarus magnus*) and a microphytophage (*Damaeus clavipes*) which indicate that, in both cases, the P parameter is distinctly in excess of the R. Possible reasons for this, and its ecological significance, are discussed.

RÉSUMÉ

Après une revue brève de la littérature concernant la biologie de la nutrition chez les Acariens Oribates, l'auteur présente un tableau des enzymes carbohydrasiques isolées à partir de ces microarthropodes. Des chiffres sont avancés pour estimer les taux de consommation de nourriture ; entre 1 et 13 %

du poids sec sont ingérés par jour. L'efficacité d'assimilation varie entre 10 et 66 %, le plus grand nombre se situant vers les pourcentages les plus élevés. Le Q10 chez les Oribates varie de 2 à 6 avec une moyenne de 3,63. L'énergie dissipée au cours du métabolisme des Oribates dans la plupart des écosystèmes terrestres est relativement basse entre 2 et 10 kilocalories par mètre carré et par an. L'auteur a établi les budgets énergétiques totaux pour une microphytophage (*Steganocarus magnus*) et un microphytophage (*Damaeus clavipes*) d'où il ressort, dans les deux cas, que le paramètre P est distinctement en excès par rapport au paramètre R. Diverses raisons sont possibles pour expliquer ce résultats et l'auteur s'est préoccupé de sa signification écologique.

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